Studying synchronization to a musical beat in nonhuman animals

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Abstract: The recent discovery of spontaneous synchronization to music in a nonhuman animal (the sulphur-crested cockatoo *Cacatua galerita eleanora*) raises several questions. How does this behavior differ from non-musical synchronization abilities in other species, such as synchronized frog calls or firefly flashes? What significance does the behavior have for debates over the evolution of human music? What kinds of animals can synchronize to music, and what are the key methodological issues for research in this area? This paper addresses these questions and proposes some refinements to the "vocal learning and rhythmic synchronization hypothesis."

INTRODUCTION

Music is often regarded as a uniquely human phenomenon.[1] Yet many components of music cognition may have deep roots in brain functions shared with other species.[2] For example, the perception of certain pitch combinations as sounding rough (e.g., two pitches separated by a semitone, such as C and C#) likely has its origins in the mechanics of the peripheral auditory system of vertebrates. Hence all primates probably perceive such roughness,[3] though humans may be the only primates that form aesthetic preferences based on this percept.[4,5,6]

The study of musically-relevant abilities in other species can thus address the evolutionary and neural foundations of human musical abilities. One such ability is beat perception and synchronization (BPS), defined as the ability to perceive a beat in music and synchronize bodily movement with it. BPS is a human universal: every known culture has some form of music with a periodic beat to which listeners synchronize their movements (e.g., in dance).[7,8] This response to music is not commonly observed in other animals. Recently, there has been growing interest in finding out whether BPS is a uniquely human ability, possibly reflecting a biological adaptation for music-making.[9,10,11]

Hence many researchers were intrigued by a 2007 video of a sulphur-crested cockatoo (*Cacatua galerita eleanora*) dancing to music. In this video, the bird (named "Snowball") was apparently synchronizing his movements (including head bobs and foot steps) in clear relation to the musical beat. This was the first inkling that a nonhuman animal could synchronize to music. Soon thereafter, we conducted a controlled experiment with Snowball, involving suppression of human movement (to avoid rhythmic cueing) and manipulation of musical tempo. We found that Snowball exhibits genuine synchronization to a musical beat, and that he can synchronize at several different musical tempi spanning a range from 106 to 130 beats per minute.[12] Due to the popularity of Snowball's dancing on the internet (e.g., on YouTube), many other pet owners have posted videos of their parrots moving to music (in fact, the website BirdChannel.com recently hosted the world's first bird dance contest). Hence it appears that Snowball is not unique,[13] and that BPS is not the sole province of humans.

The details of our experimental study (first presented at *The Neurosciences and Music III*, June 2008, Montreal) will appear in a forthcoming scientific article. Rather than repeat those details here (some of which can be found in ref 12, available at http://www.nsi.edu/users/patel, together with video examples), the current paper takes a broader view and discusses four issues relevant to the study of BPS in other species. This is a new topic in music cognition, involving (so far) studies of birds and bonobos.[12,13,14]

First, what distinguishes musical BPS from synchronized rhythmic displays in other species? Second, what significance does nonhuman BPS have for debates over the evolutionary status of music? Third, how do current findings help refine the hypothesis that BPS builds on the brain circuitry for complex vocal learning?[15] Fourth, what are some key methodological issues for research in this area? The following sections consider these issues in turn.

BPS VS. SYNCHRONOUS ANIMAL DISPLAYS

At first glance, BPS may not seem that special. Many species are known to engage in rhythmic synchronized acoustic or visual displays. The synchronous flashing of certain firefly species is a well known example.[16,17] Other examples include rhythmic chorusing in frogs and katydids.[18,19] A closer examination of such displays, however, suggests that they differ from BPS in important ways (Table 1). First, BPS typically involves extracting a regular beat from a very complex signal (namely, music), rather than from simple pulse trains. Second, BPS involves substantial flexibility in movement tempo: humans adjust the rate of their rhythmic movements to synchronize to music across a wide range of tempi. Third, BPS is truly cross-modal, with an auditory stimulus driving the motor system in periodic behavior that it not (necessarily) aimed at sound production. To our knowledge, no animal displays have this combination of features. These differences between BPS and nonhuman animal displays argue against the view that synchronization to a musical beat is a minor variant of synchronization abilities of other species. Instead, BPS appears to be an unusual behavior in the animal kingdom, raising questions about its evolutionary origins and significance.

Table 1: General features of pulse-based synchronization vs. BPS (beat perception and synchronization)

	Pulse-based synchronization	**BPS (Beat perception and synchronization)**
Stimulus complexity	Low Metronome-like pulse trains	High Rhythmically and / or melodically complex signals
Tempo flexibility	Narrow Limited tempo range of rhythmic actions	Wide Broad tempo range of rhythmic actions
Response modality (compared to input)	Same e.g., flashing in response to rhythmic flashes	Different e.g., silent rhythmic movement in response to sound

THE EVOLUTIONARY SIGNIFICANCE OF BPS IN OTHER SPECIES

There is currently an active debate whether human music is a product of biological evolution, or an invention built on brain systems which evolved for other purposes.[11,20,21] BPS is important in this debate, because it is central to music cognition and is not an obvious byproduct of other human cognitive abilities, such as language.[15] Is BPS a biological adaptation for music?[22,23] This question can be addressed by comparative research with other species. If other animals (whose brains have not been shaped by natural selection for music) are capable of BPS, this would argue against the view that BPS reflects natural selection for music.

In this light, the discovery of BPS in a sulphur-crested cockatoo is particularly interesting. This species (native to Australia and New Guinea) is not known for melodious vocalizations or for complex dancing in courtship displays. According to Forshaw, the courtship display "is simple and brief. The male struts along a branch towards the female. With crest raised he bobs his head up and down and swishes it from side to side in a figure-eight movement, uttering soft, chattering notes all the while (p. 131)."[24] Of course, in species with complex, melodious songs[25] or elaborate courtship dances,[26] one might argue that musically-relevant abilities have been shaped by natural selection. In sulphur-crested cockatoos, however, such arguments seem unlikely to apply, making it plausible that that BPS is a byproduct of some non-musically-relevant ability. What is this ability? As outlined in the next section, one possibility is complex vocal learning.

Before turning to that section, however, it is worth discussing the evolutionary relationship between avian and human BPS. At one level, the relationship is clearly one of convergence, i.e., the historically independent evolution of a trait in distinct lineages of organisms. However, if the vocal learning hypothesis is correct, and if vocal learning circuitry in birds and humans has common neural foundations (as argued in ref 27), then BPS in the two species has a relationship in terms of underlying biological mechanisms. This would make it a case of "deep homology",[28] and indicate that neurobiological studies of BPS in birds could shed light on mechanisms of BPS in humans. The practical significance of this possibility is discussed in the final section of the paper.

REFINEMENTS TO THE "VOCAL LEARNING AND RHYTHMIC SYNCHRONIZATION HYPOTHESIS"

Patel[15] proposed that BPS builds on the brain circuitry for complex vocal learning, i.e., learning to produce complex acoustic communication signals based on imitation. This "vocal learning and rhythmic synchronization" hypothesis was motivated by three observations. First BPS involves a special auditory-motor interface in the nervous system, as evidenced by the fact that people synchronize much more poorly to the beat of visual vs. auditory rhythms matched in temporal structure.[29] Vocal learning creates a tight auditory-motor interface in the brain, since it involves integrating auditory perception with rapid and complex vocal gestures. Second, vocal learning in birds involves modifications to brain regions (such as the basal ganglia[30]) which are also likely to be involved in vocal learning in humans, based on comparative neuroanatomical research.[27] Third, neuroimaging research suggests that some of these same regions are involved in human beat perception in music.[31]

A testable prediction of the vocal learning hypothesis is that only vocal-learning species are capable of BPS. (Notably, humans are unique among primates in having complex vocal learning, an evolutionarily rare trait shared by only a few groups of animals, including humans, parrots, songbirds, hummingbirds, dolphins, seals and some whales.[32,33] Some provisional support for this hypothesis has been provided by Schachner et al.,[13] who surveyed numerous videos of animals moving to music (on YouTube) and found that all species which appeared to move in synchrony with the musical beat (n=28) were vocal learners. (This finding naturally calls for replication using controlled experiments to rule out imitation of rhythmic movements by humans, who might have been dancing off camera.)

As originally stated, the vocal learning hypothesis claimed that vocal learning was a necessary foundation for BPS. However, vocal learning may not be the only necessary foundation. Parrots share more than just vocal learning with humans. Table 2 lists some traits shared by these species.

Table 2: Traits shared by parrots and humans

Trait	**Comment**
Complex vocal learning	A rare ability in the animal kingdom,[33] and unique to humans among primates.[34]
Open-ended vocal learning	The ability to acquire complex new sound patterns throughout life. Some songbirds can also do this (e.g., Starlings), but many cannot.[25,35]
Non-vocal movement imitation	Convincing evidence for this ability is rare in other species, and has been provided for parrots, chimps, and dolphins.[36]
Living in complex social groups	A trait may that have consequences for brain size and organization.[37]

At this point, it is not clear what traits in Table 2 might be necessary foundations for BPS. The vocal learning hypothesis states that complex vocal learning is a necessary foundation, and hence predicts that chimps and bonobos (who share only the third and fourth traits in the table with humans) are incapable of BPS. However, it may be that complex vocal learning is not enough, and that open-ended vocal learning (and its concomitant brain substrates) is also necessary. Only comparative work with other species can resolve this question. For example, starlings have open-ended vocal learning,[38] and are thus a logical choice for testing an open-ended vocal learning hypothesis for BPS. If Starlings are not capable of BPS, however, then it may be that open-ended vocal learning **and** non-vocal movement imitation are necessary foundations for BPS, a hypothesis that could be tested with dolphins (who share all traits in table 2 with humans).

Stepping back, the fundamental question that needs to be addressed by comparative research is "What kinds of brains are capable of BPS?". Such work can help identify the evolutionary foundations of BPS in humans.

STUDYING BPS IN OTHER SPECIES: ELEVEN METHODOLOGICAL ISSUES

Since the study of nonhuman animal (henceforth, "animal") synchronization to music is a new research area, it is worth discussing a number of methodological issues relevant for those planning to conduct (or evaluate) research in this area.

1. What are the criteria for synchronization?

Humans BPS involves movements that match the musical beat in both tempo and phase.[39] These two criteria are conceptually distinct. Tempo matching means that the period of rhythmic movement matches the musical beat period, without regard to relative phase between movements and beats (for example, movements might be in antiphase with the beat, i.e. clustered around a time point midway between beats). Phase matching means that rhythmic movements occur near the onset times of musical beats (zero phase). Hence when testing for rhythmic entrainment it is important to specify whether one is testing only for tempo matching, or for both tempo and phase matching. Different statistical tests are required in the two cases. One test (based on circular statistics) which is sensitive to both tempo and phase matching is the Rayleigh test specified for mean direction (see equation 4.15 on p. 69 of ref 40).

2. How complex is the stimulus?

As noted previously, synchronization to pulse trains is seen in numerous species (e.g., fireflies and frogs). BPS, in contrast, typically involves extracting a regular beat from signals rich in rhythmic and melodic complexity (e.g., real music). Hence demonstration of animal synchronization with metronome-like stimuli, while interesting, is not the same as demonstrating BPS (cf. Table 1).

Conversely, if an animal demonstrates BPS there is no guarantee that the same animal would synchronize with metronome-like stimuli. While the ability to synchronize to simple pulse trains is implied by BPS, such behavior may not be easy to elicit if the pulse trains do not sustain the animal's interest or attention.

3. How flexible is the tempo of the animal's rhythmic movements?

A key feature of BPS is tempo flexibility. Humans adjust the tempo of their rhythmic movements (e.g., foot taps) to synchronize with music across a wide range of tempi. Hence if an animal synchronizes its movements to a musical beat, it is important to establish whether it can adjust the tempo of its movements when the music is played at different tempi. The use of different tempi also rules out coincidental matches between the musical tempo and the animal's natural frequency of movement.

4. What modality is the response?

Very often, human BPS often involves movements which are not aimed at sound production. For example, head bobbing, finger tapping, and dancing are not usually aimed at making sound. Thus if an animal synchronizes movements to music, it is important to ask if this is only done in the context of making sound (e.g., striking a drum or some other musical instrument), or if it is a purely motor response.

5. How well were visual rhythmic cues controlled?

Humans tend to move to music, and can thus inadvertently give rhythmic cues to the beat to animals (e.g., subtle head bobs). This is a particular concern in studies of parrots and chimps/bonobos, who are capable of imitating non-vocal movements.[36] Studies which seek to demonstrate BPS in animals need to eliminate possible visual rhythmic cues from humans involved in the experiments. This can be done via verbal instructions to humans (e.g., to avoid head bobbing). Even better is having video footage of any humans in the room during experimental trials, so that human movements can be checked for possible subtle rhythmic cues. The best control, of course, is to have no humans in the room. For example, humans could be outside the room giving verbal encouragement over speakers, but while listening to masking stimuli so that verbal cues are not in time with the music. (The absence of a human in the room, however, may influence the animal's motivation to dance.)

6. Can the animal synchronize to novel music?

Humans easily synchronize to the beat of novel music. If an animals' synchronization to music is strongly stimulus-bound (e.g., only observed to a particular piece of music), this would point to an important difference between animal synchronization and human BPS.

7. How much training was required?

BPS emerges relatively spontaneously in humans. Children's early experiences in being bounced rhythmically to music,[41] observing others moving to the beat of music, and being socially rewarded for their own dancing may play a role in the development of BPS, but it is clear that human BPS develops without elaborate, explicit instruction (unlike, say, reading and writing). Thus in studying BPS in animals, it is important to document how the behavior emerged. What role did modeling and reward play? Was an extensive training period required, or did it emerge more spontaneously? In this regard, it should be noted that if an animal does not demonstrate spontaneous BPS, this may reflect a lack of interest or attention rather than a lack of ability. Studies which aim to discover whether an animal is capable of BPS need to take motivational factors into account.

It is interesting to note that Snowball's BPS abilities emerged relatively spontaneously. His previous owner acquired him at a bird show when Snowball was 6, and mentioned that soon thereafter he noticed Snowball bobbing his head to rock music (the owner felt that this was not done in imitation of human movement). Subsequently, the owner and his children began to encourage Snowball's dancing, partly by making rhythmic arm gestures to the beat of the music. Snowball quickly developed his own rhythmic foot-lifting behavior, perhaps in imitation of the human arm gestures. Hence his dancing behavior was not a product of deliberate training, nor was he trained to dance using food rewards.

8. Is the synchronization mutual or one-way?

In recent research on bonobo synchronization to music, an interactive approach was used in which human and bonobo played rhythmic chords on separate keyboards at the same time, usually out of view of each other.[14] During periods when both participants played at stable tempi the degree of synchrony between human and bonobo was quantified. In this "mutual synchrony" approach, an important question concerns to what extent such synchrony reflects the human adapting to the animal's timing, rather than vice-versa. This is a particularly salient issue because humans have been shown to adjust the phase of their rhythmic tapping in response to changes in the timing of an external pacing stimulus, without their own awareness.[42] Hence when studying mutual synchronization between human and animal, statistical methods are needed to tease apart the degree to which entrainment reflects human (rather than animal) synchronization. Notably, human BPS need not be interactive: humans are quite capable of synchronizing to music in a "one-way" fashion in which the human responds to the music but not vice versa (e.g., when dancing to recorded music). Hence an important question for animal BPS studies is whether the animal being studied is capable of one-way synchronization.

Of course, this is not to say that the role of interaction and social cues should be neglected in research on animal BPS. On the contrary, there are good reasons to study these issues. For example, it has recently been demonstrated that young children are better at synchronizing to a steady beat in a social vs. nonsocial context.[43] This naturally raises the question of whether the same is true for animals. This can be addressed, for example, by measuring whether an animal synchronizes with music better when moving jointly with a human than when moving alone.

9. What is the relationship to the animal's natural display behavior?

Many animals make rhythmic movements as part of ritualized displays. Chimps perform brief bouts of drumming on the buttresses of trees,[44] and a number of bird species perform elaborate "dances" as part of displays aimed at conspecifics.[26] Hence when studying animal BPS, a question of interest concerns the relationship of the observed rhythmic movements to natural display movements. Specifically, does BPS involve adapting an existing display behavior, or does it represent a novel movement sequence not seen in the animal's natural display repertoire?

10. Are there hierarchical levels of rhythmic movement?

Much music has a hierarchical rhythmic structure, whereby there are not only regular beats, but also regular patterns of accentuation among beats which create a metrical hierarchy.[45] For example, in a march every second or fourth beat may be accented. Human movements associated with BPS shows evidence of sensitivity to such structure.[29] If an animal exhibits BPS, it is of interest to know if the rhythmic movements mark only one level of the metrical hierarchy, or if there is evidence for sensitivity to multiple levels.

Snowball's dancing is notable in this regard because he sometimes moves his head from side to side on every other beat, while simultaneously bobbing his head with each beat. This suggests sensitivity to the hierarchical rhythmic structure of beats in music, though further work is needed to determine whether the side-to-side movements have any systematic relationship to the metrical structure (e.g., if they tend to mark out beats 1 and 3 in each measure of a 4/4 time song, as these are the stronger beats in the measure).

11. Could it have happened by chance?

A key issue for animal studies of BPS is whether the observed synchronization is merely a coincidence. This question is particularly important when synchronization to music is transient, as in our study of Snowball. That is, even when Snowball danced rhythmically during an entire experimental trial, there were limited periods when he showed genuine synchronization to the beat. (He may resemble human children more than human adults in this regard.)[46] This is illustrated in Figure 1a, which shows the tempo of Snowball's rhythmic movements (head bobs) during one experimental trial (about 70 seconds, music tempo = 106 BPM).

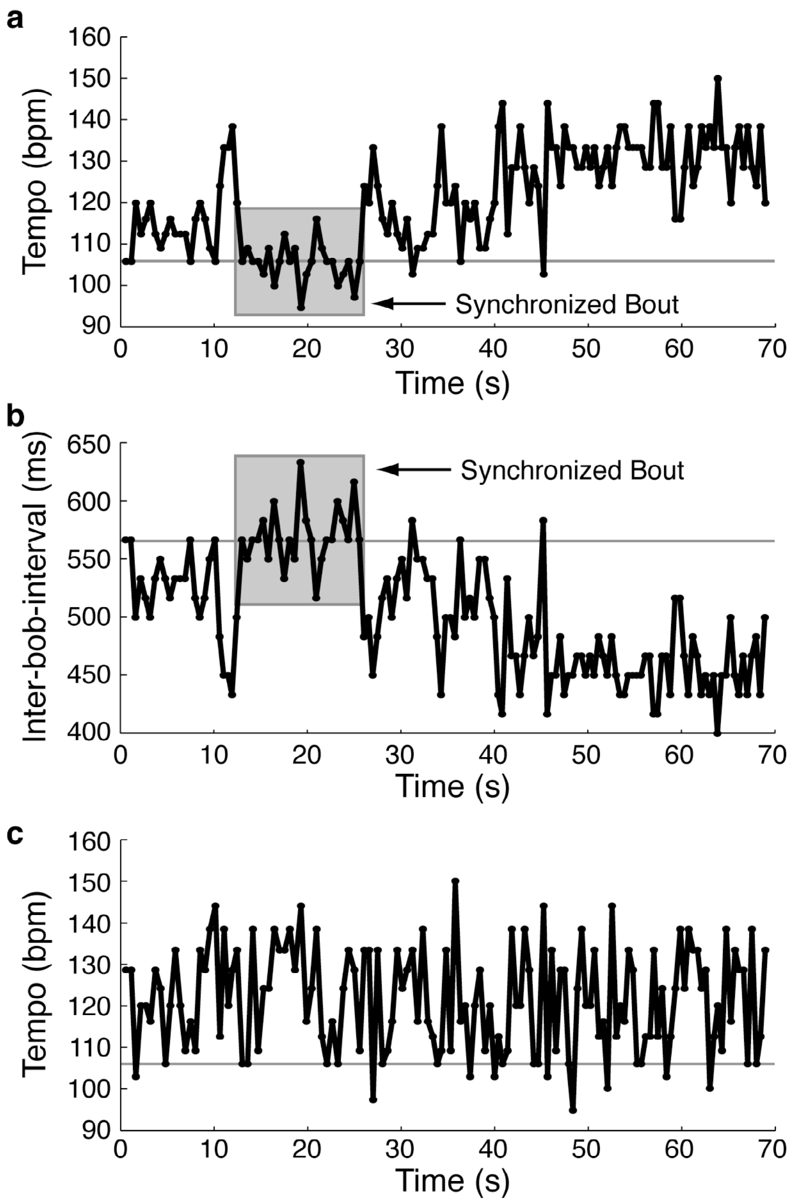

Figure 1. Time series illustrating real (a,b) and time-scrambled (c) measurements of the timing of Snowball's rhythmic movements during one experimental trial in which the musical tempo was 106 beats per minute (BPM). Temporal measurement of rhythmic movements was based on head bobs (see ref 12 for details). Panel (a) shows Snowball's dance tempo in BPM, while panel (b) shows the same data converted into temporal intervals between head bobs (musical tempo in all graphs is indicated by the thin grey horizontal line). In panels (a) and (b) the inset shaded box indicates a synchronized bout. Panel (c) shows a tempo curve generated by randomly scrambling the time points in panel (a). Note the lack of slow drift in (c), compared to (a).

The inset box shows the time during which he showed a synchronized "bout" (a period of sustained synchronization to the beat, see ref 12 for details). During this bout, his tempo matched the music tempo and the timing of head bobs was very close to the timing of musical beats (i.e., entrainment near zero phase, as seen in human movement to music).

As is clear from the figure, however, the synchronized bout accounts for only about 20% of the entire trial. Across the trial Snowball shows substantial tempo drift. For example, towards the end of the trial he drifted toward a tempo of about 130 BPM. (This was frequently observed across trials, suggesting that he has a preferred tempo for rhythmic movement, just as humans do.)[47] Because his synchronization to music is transient, statistical methods are needed to estimate the probability that such episodes could have happened by chance. That is, one must consider the null hypothesis that the animal moves rhythmically in response to music, and that due to natural variability in movement tempo there are periods when (by pure chance) the movements have a consistent relationship to the beat. Our methods for dealing with this problem are discussed in detail in our forthcoming scientific article on Snowball. For the moment, we simply discuss one seemingly intuitive way of dealing with the problem.

This is the approach of scrambling the order of the temporal intervals between rhythmic gestures (e.g., head bobs) within a trial, and then recomputing synchronization measures. If this is done repeatedly (e.g., 1,000 times), one can compute the probability of observing the actual degree of synchronization (e.g., in the case of Figure 1a, how often does one observe a synchronized bout lasting 20% or more of the trial?). At first glance, this Monte-Carlo approach seems attractive for its conceptual simplicity.

Figures 1b-c, however, indicate why this approach is unsatisfactory. Figure 1b shows the inter-bob-intervals corresponding to the tempo curve in Figure 1a (that is, Figure 1b re-represents the data in Figure 1a in a more conventional way for rhythm studies, namely as time intervals between successive rhythmic gestures). Randomly scrambling these time intervals and converting them back to a tempo curve produces the time series in Figure 1c. As can be seen, the resulting curve has a very different structure from the curve in Figure 1a. Specifically, the original curve shows fast local tempo fluctuations superimposed on a slower pattern of tempo drift. The curve produced from scrambled data, in contrast, lacks the slow tempo drift and is thus not representative of how the animal actually moves. Hence doing synchronization tests on scrambled data is not a fair test of the null hypothesis mentioned above.

Stepping back from these details, the important point is that to test the null hypothesis of no true synchronization to music, one must use data that statistically resembles the movement pattern produced by the animal under study. Using simulated data that is unlike actual animal movement patterns (e.g., Figure 1c) is not adequate for testing the null hypothesis of no true synchronization to a musical beat.

BROADER SIGNIFICANCE

As the study of animal synchronization to music gets underway, it is worth asking what broader significance such research has for human concerns. Apart from addressing debates over the evolution of music (as outlined in this paper), such research has potential practical significance. This is because BPS has a powerful impact on the human motor system, as documented by music therapy researchers For example, some patients with Parkinson's disease can become "unfrozen" and able to walk when they synchronize their movements with a musical beat.[48,49] The mechanisms behind this, however, remain mysterious.

Other species have simpler brains than we do. If it can be shown that nonhuman animals move to music in much the same way as humans do, and if this movement is based on similar brain mechanisms as in humans, this would open the way to comparative neural studies of the biological foundations of BPS. That is, having an animal model of BPS would give scientists a new approach to studying this remarkable ability and its power to alleviate human movement disorders.

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